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BIOLOGICAL STUDIES OF *DISSOSTEIRA SPURCATA* SAUSSURE with Distributional Notes on Related California Species^{1,2} (Orthoptera-Arididae)

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INTRODUCTION

STUDIES OF THE biology and ecology of range land grasshoppers have, with a few notable exceptions, been badly neglected. This is exemplified in the genus *Dissosteira* where a considerable amount of biological information exists for *D. carolina* and *D. longipennis* but little or none for the other two species in the genus, *D. pictipennis* and *D. spurcata*. Much of this neglect can be attributed to one or more of the following factors: many species of grasshoppers involved; the inhospitable country inhabited by most; lack of injury to cultivated crops by most species; and, until the introduction of the chlorinated hydrocarbon insecticides, the lack of appreciation of the damage caused to range lands. The large areas involved and the expense of controlling range land grasshoppers on low unit value land have also militated against a thorough knowledge of these species.

The spureate grasshopper, while common and widespread in many areas of the West, is rarely the dominant species in a mixed population of grasshoppers. Ordinarily, in northern California, it ranks no higher than fourth or fifth from the top in order of abundance. In any given area at least two other species, particularly *Oedaleonotus enigma* and *Melanoplus devastator*, usually are present in greater numbers. Thus *spurcata* has frequently been overlooked, with attention focused on the more numerous and obvious species present.

D. spurcata is hardly to be considered by itself as having any significant economic importance, but along with many other species of grasshoppers adds its share to the damage caused to the range land each year.

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In addition to the obvious plant consumption, *D. spurcata*, along with associated species of grasshoppers, causes losses which may not be immediately apparent. On deteriorated range where it is a typical inhabitant, it would with other grasshoppers, make reseeding of more desirable grasses very difficult. A good example of this was presented at the Hopland Range Experiment Station in 1957. A field seeded with Hardinggrass showed very heavy feeding on this particular plant by *M. devastator*, *C. pellucida*, and *D. spurcata*. So many of the plants were consumed, sheep could no longer feed. This species is seldom found in cultivated crops, preferring to remain on the range lands in small numbers and displaying no tendency to migrate.

TAXONOMIC STATUS OF *DISSOSTEIRA SPURCATA* SAUSSURE

Scudder (1876),⁵ in his report of Orthoptera collected by Lt. Wheeler's geographical survey party in 1875, first described the genus *Dissosteira* which he separated from Latreille's (1825) genus *Oedipoda*. He stated that *Dissosteira*, of which *Gryllus carolinus* L. is the type, differs from the true *Oedipoda*, as represented by its type *Gryllus caerulescens* L. He enumerated the morphological differences and pointed out that in most of the characters the group approaches much more closely the American rather than the Old World group of the *Oedipoda*. At the same time he placed *Oedipoda nebrascensis* Brun. (= *D. longipennis* Thomas) in *Dissosteira*.

Thomas (1880) first described *spurcata* as *Oedipoda oblitterata*, either ignoring or being unaware of Seudder's new genus *Dissosteira*. The combination *Oedipoda oblitterata* was preoccupied, however, having been first used by Germar (Burmeister, 1838) for the grasshopper now known as *Pardalophora apiculata* (Say). Saussure (1884), apparently unaware of Thomas' description of *O. oblitterata*, described it as *D. spurcata*. The latter name must be used since *O. oblitterata* Thomas is a primary homonym of *O. oblitterata* Germar.

Bruner (1893) in his list of destructive locusts of America used the name *D. oblitterata* for *D. spurcata*. This synonym, however, was not widely used and was subsequently corrected in his 1905 publication.

Although several common names have been used in the past for *D. spurcata*, such as Urbahns (1920) calling it the foul grasshopper, there is at present no accepted common name; it is therefore suggested that the name "spurcate grasshopper" be used for this species.

The spurcate grasshopper has been listed or merely mentioned by Essig (1956), LaRivers (1948), Bruner (1897; 1905), and Scudder (1900; 1901). Rehn and Hebard (1906; 1909) wrote about color and size variations, while Rockwood (1925) described this species fluttering like moths around lights in Boise, Idaho. It has also been briefly mentioned by Coquillett (1885; 1892), Urbahns (1920), Harper (1950; 1952a; 1952b) and California Cooperative Insect Report (1958). Henderson (1924; 1931), in two papers on the Orthoptera of Utah, described and discussed *D. spurcata* more fully. Middlekauff (1959) briefly discussed the male nuptial flight.

⁵ See "Literature Cited" for citations referred to in the text by author and date.

METHODS AND MATERIALS

Colonies of *D. spurcata* were maintained in the laboratory throughout the spring, summer, and early fall during the two years of this study. All of the rearing was done at the University of California Insectary located at Berkeley, California. Maintenance of these colonies facilitated observation of the habits and actions of this species as well as permitted more precise studies of growth rate, survival, and longevity at different temperatures. In the second year of study, egg masses marked the previous year were collected and then refrigerated to break the diapause. The eggs were permitted to hatch under approximately natural conditions and the nymphs were reared under controlled temperatures. The techniques of Shotwell (1941) were used; he had successfully reared 12 species occurring in the northern Great Plains area. While much work with this species was done in the laboratory, most of the data were collected by frequent trips to the field where normal conditions and reactions prevailed.

Nymphs were collected by placing an open aerial insect net in front of them and causing them to jump into it. Adults were netted on the ground.

Eggs were collected by marking the observed oviposition sites with small stakes and later sifting the soil for the egg pod. A few eggs pods were obtained from caged females.

The eggs obtained from both cage and field oviposited egg pods were placed in tin salve boxes and then in turn were placed under refrigeration at about 40° F for several months to break the diapause. The egg pods were then broken apart and 20 single eggs were placed in each of a number of clay nursery pots. The pots were filled with sterilized soil and the eggs placed 1 to 1½ inches below the surface. The pots were covered with an open-bottom cylinder of 14-mesh wire screen. In order to maintain the proper degree of moisture in the soil for hatching, the pots were corked and partially buried in a sand table in the greenhouse. The sand table was watered regularly and with one exception the moisture in the pots remained suitable for hatching. As the nymphs hatched, they were placed in the individual cages and these were then placed in the controlled temperature cabinets. Alfalfa, lettuce, or clover was fed daily to all caged grasshoppers.

The cages used in room-rearing had unfinished redwood frames covered with 24-mesh wire screen. They were 16 inches wide, 17 inches deep, and 19 inches long. The top piece of wire could be lifted in front to permit manipulations inside the cage. The open bottom of the cage was covered with a sheet of aluminum foil upon which was placed a 2-inch deep plastic dish containing soil. The dish could easily be removed for cleaning and the soil sifted for eggs. Sand, first used in the dish, proved to be unsatisfactory to ovipositing females. A mixture of half sand and half soil likewise was not completely accepted. Soil covered with gravel and rock taken from the study area proved to be most satisfactory. The presence of these rocks stimulated mating and oviposition of eggs in the soil rather than in foamy masses on the wire screen.

The cages used for individual rearing in the temperature cabinets were constructed from cylindrical, pint-sized ice cream cartons. Windows were

cut in the sides and covered with a fine nylon mesh; the top was also covered with the nylon material with the outer rim retained to secure it. This small cage was necessary since space was at a premium in the temperature cabinets. This cage also allowed for easy cleaning, feeding, and handling of the small, developing nymphs. The nylon material was also used as a support during molting. The nymphs would hook their hind legs into it and have a firm base for the molting procedure.

It was important to have only a minimum of actual contact in handling the small, delicate nymphs. Forceps cause injury, particularly to the hind legs which come off quite easily. It was best to place a glass vial over the nymphs, tilting the cage and gently tapping the surface on which they stood. The nymphs either jumped or fell to the bottom of the vial, where they were held while the cage was cleaned or new food provided. Adults were most easily handled by grasping the tegmina with forceps.

During the first summer of rearing, lettuce, grasses, and occasionally other leafy green vegetables such as cabbage were fed. The nymphs and adults survived fairly well on this diet. However, during the second summer, alfalfa was included in the diet and seemed to add considerably to the health and development of the grasshoppers. Barnes (1955) in testing the effect of various foods on the lesser migratory grasshopper, *Melanoplus bilituratus* (Walker), found that alfalfa in the diet increased longevity, but if used exclusively it was a very unfavorable food compared with mixed diets. Water was available from the foods, but in addition small vials of water with cotton wicks were placed in the cages.

The heat for the large cages used in room-rearing was provided by 60-watt electric light bulbs in gooseneck lamps placed on each side of the cage, shining downward from the top. They could be moved to give light in any direction desired. Fluorescent electric lights did not provide sufficient heat for the cages. The grasshoppers tended to congregate near the source of heat, clinging to the sides and top of the cage. By using the lamps, night-time temperature of about 86° F and day-time temperature of about 93° F were maintained. When desired, the lamps could be moved closer or farther away, whichever was required. Relative humidities were 50 to 60 per cent at night and 30 to 50 per cent in the day time. The food and water provided in the cage will normally maintain an adequate humidity.

In the constant temperature studies the three temperatures used were 68°, 77°, and 89.6° F. The temperature cabinets used were checked regularly to maintain the desired conditions and hygrothermograph readings were taken showing a relative humidity of 48 to 52 per cent for the 68° and 77° F cabinets and a 38 to 40 per cent relative humidity for the 89.6° F cabinet.

DISTRIBUTION OF SPECIES IN THE GENUS *DISSOSTEIRA*

The genus *Dissosteira*, as it now stands, is composed of four⁶ species restricted to Nearctic America: *carolina* (L.), *longipennis* (Thomas), *pictipennis* Bruner, and *spurcata* Saussure. The high plains grasshopper (Wakeland, 1958), *D. longipennis*, is the only member of the genus not found in California.

⁶ Gurney and Strohecker (1959) have shown that *D. planipennis* Bruner is a synonym of *Microtes occidentalis* (Bruner).

The distribution of the various California species is shown on maps 1 to 3. These are based upon data from the following sources: specimens in private or institutional collections as enumerated in the acknowledgments; published records considered reliable; and specimens collected by the authors in central and northern California.

D. carolina has the widest distribution, being found throughout much of the United States, Canada, and Nova Scotia. It has been recorded from every



Map 1. General distribution of *Dissosteira carolina* (Linn.) in California counties.

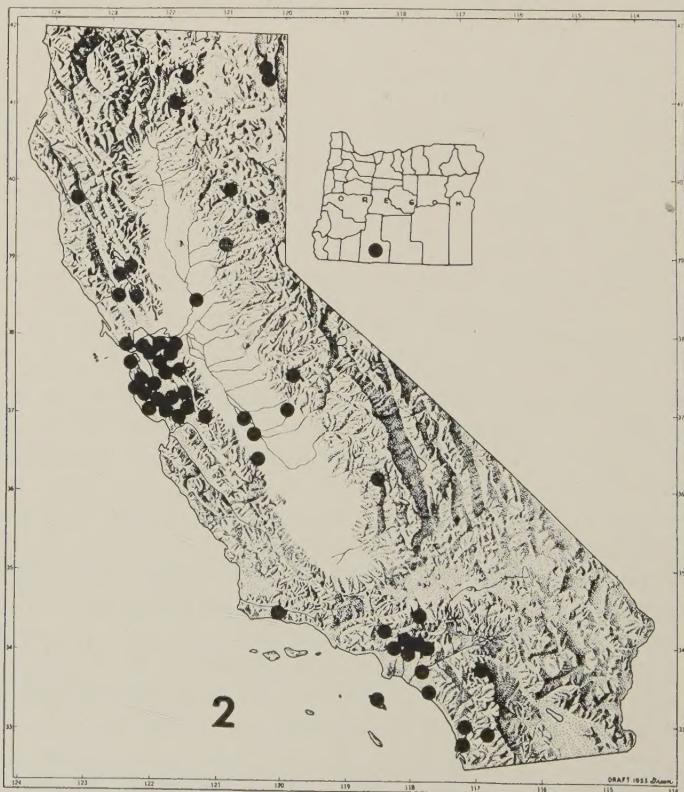
state except Hawaii and Alaska. It is most common in the Great Plains and Rocky Mountain states and occurs only infrequently in California (Map 1). Newton and Gurney (1957) have shown the distribution of *carolina* for the United States.

*Dissosteira pictipennis*⁷ Bruner is a distinctive red-winged species, widely distributed in California. It has also been recorded from southern Oregon and from Santa Catalina Island off the coast of southern California (Map 2). With the exception of several collections along watercourses in the Central Valley this species is confined to range lands. It appears to favor a higher habitat than does *spurcata* and is seldom in association with it. In the central coastal area, it is found widely scattered in the oak-grassland habitat in low numbers. It shows little tendency to congregate or to migrate.

⁷ According to Rehn (1945) Stål first named this species *venusta* in 1861 but since the name was already occupied by a Greek species it was unavailable. The first subsequent name was *pictipennis* Bruner.

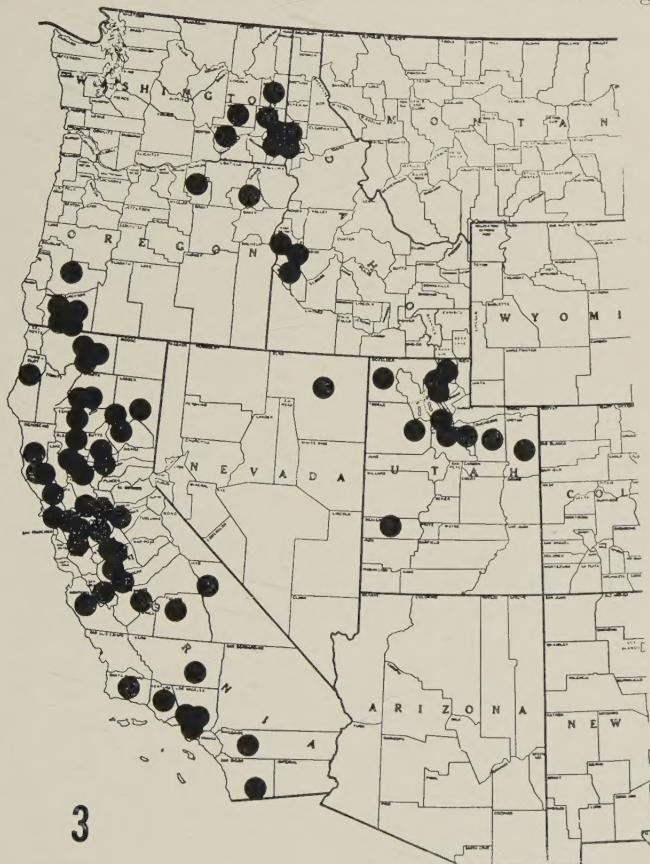


Fig. 1. Range land area showing typical habitat of *Dissosteira spurcata*. Notice sparse vegetation and gravelly, rocky soil.



Map 2. Distribution of *Dissosteira pictipennis* (Bruner). Insert map shows a single collection record for Oregon. Each circle indicates a locality record.

Dissosteira spurcata Saussure has been recorded from the following western states: California, Idaho, Nevada, Oregon, Utah, and Washington (Map 3). In central and northern California it frequents the oak-grassland association of the Upper Sonoran (lower foothill belt) and Lower Sonoran (valley) life zones of Merriam's (1898) classification. Within this range, clovers,



Map 3. Distribution of *Dissosteira spurcata* Saussure, the spurcate grasshopper.
Each circle indicates a locality record.

filaree, and annual grasses are dominant. This is the range land area which averages between 7 and 15 inches of rainfall per year.

D. spurcata prefers a well-drained, hot and dry area that contains sparse or spotty vegetation with a rocky or graveled layer over the soil (fig. 1). It appears to be most abundant on deteriorated, over-grazed ranges. They are almost always associated with or in close competition with several other species of rangeland grasshoppers in central and northern California, particularly *Melanoplus devastator*, *Oedaleonotus enigma*, *Cannula pellucida*, and one or more species of *Trimerotropis*.

D. spurcata has been observed, collected, and studied by the writers in the following areas of northern California:

TABLE I
PRECIPITATION DATA—MIDWAY ROAD STUDY AREA,
U.S.W.B. TRACY PUMPING PLANT, ALAMEDA COUNTY, CALIFORNIA

* Tracy Pumping Plant station established February, 1955.

TABLE 2
TEMPERATURE DATA (DEGREES F)—MIDWAY ROAD STUDY AREA.
U.S.W.B., TRACY PUMPING PLANT, CALIFORNIA, 1958-1959*

All fractional degrees given as nearest whole number.

In foothill range lands north of Oroville, Butte County, between Clark Road and the Oroville-Pentz-Magalia Highway at an approximate elevation of 190 to 200 feet.

In range lands at the University of California Field Station, Hopland, Mendocino County, at elevations ranging from 800 to 3,000 feet.

In foothill range lands 1 mile east of Mission Peak, east of Mission San Jose, Alameda County, at an approximate elevation of 1,500 feet.

At Midway Road, Alameda County, where it is bisected by the Southern Pacific railroad tracks, 6 miles ESE of Altamont and 7½ miles WSW of Tracy at an approximate elevation of 400 feet.

The Midway Road area contained the largest population of the spureate grasshopper found and appeared ideally suited ecologically for this species. The principal oviposition sites and developmental areas of the younger nymphs were along both sides of the railroad bed for approximately 60 to 80 yards (fig. 2) and along the county road on both sides for 20 to 25 yards. Starting a week after hatching, there was a gradual movement of the later instars into the long grasses on either side of the tracks but a sizable population remained near the old egg bed sites. Most of the studies were undertaken in this area.

TEMPERATURE AND PRECIPITATION DATA OF THE MIDWAY ROAD (ALAMEDA COUNTY) STUDY AREA

Temperature and precipitation data were taken from the United States Weather Bureau, Tracy Pumping Plant weather station, the nearest one to the Midway Road study area. This station, at an elevation of 61 feet, is approximately 9½ miles WNW of Tracy, San Joaquin County, and 5¼ miles NNW of the Midway Road study area.

In order to give an over-all picture of the weather of the Midway Road area, a five-year accumulation of temperature and precipitation data is presented (tables 1 and 2).

As shown in table 1, the months of June, July, and August are normally nearly rainless. It is not unusual to get some rain in September but the quantity received in a one-day storm in 1959 was the second heaviest 24-hour and monthly total within the period of record keeping by the Weather Bureau in California. It was exceeded only by a September storm in 1904. The real rainy season usually begins in November or December and tapers off in April or May.

From May through November, the average monthly rainfall seldom exceeds ½ inch and the five-year cumulative average for this 7-month critical period in the life of *D. spurcata* is less than ⅓ inch per month.

During the nearly five years of record keeping at the Tracy Pumping Plant the annual quantity of rain has varied from a low of 7.67 inches in 1956 to a high of 13.14 inches in 1958.

In 1958, the first year of study in the Midway Road area, the fall rains did not come until late in December. With a total of 1.56 inches of rain in May through December, it was the driest fall in over one hundred years in California.

In general *Dissosteira spurcata* is found in those range land areas receiving

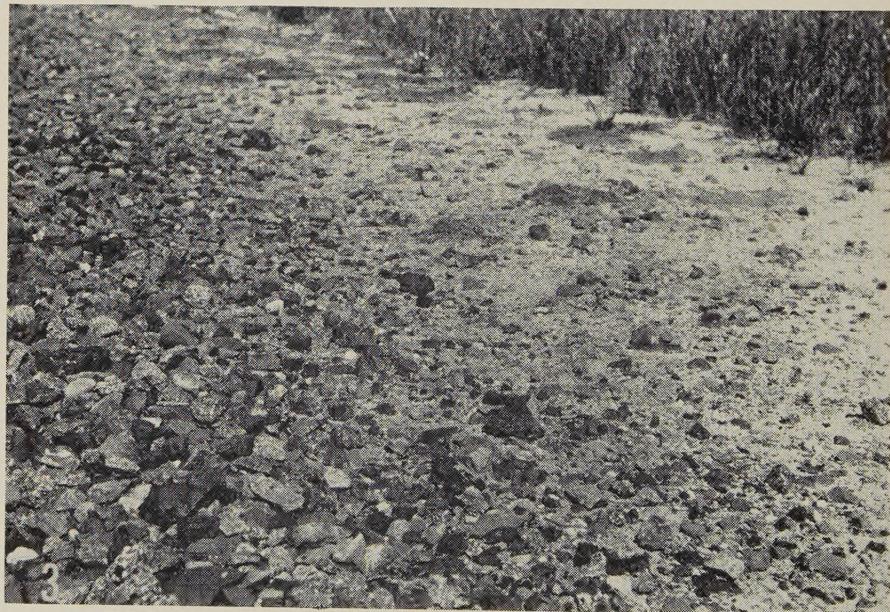


Fig. 2 (top). Panoramic view of the rocky, sparsely vegetated soil where *D. spurcata* females were found ovipositing. Midway Road area, Alameda County.

Fig. 3 (bottom). Close-up view showing composition of soil in oviposition area utilized by *D. spurcata*.

not more than 15 to 20 inches of rain per year. The rains come mostly when this species is in the egg stage, thus the nymphal and adult stages (present from April to October) would on the average not be subjected to total rainfall exceeding 2 inches.

Temperature data for the study area during 1958 and 1959 are given in table 2. It can be seen that days exceeding 90° F start in April or May and become increasingly common through August and cease again by late October. Winters are relatively mild with only a few days falling below freezing.

Average daily maximum temperatures normally exceed 75° F during the months of late April through October; and exceed 90° F during the hot months of July, August, and September. Daily maximums during June to October will exceed 100° F.

The evaporation rate in this area is exceedingly high, with strong winds almost a daily phenomenon.

As can be seen in the table, the spring months of February, March, and April, 1958, were much cooler than in 1959. This was reflected in a delayed hatch of range land grasshoppers. It was not until the last week of April that *spurcata* began hatching. In 1959 the warmer weather brought on the hatch early in the second week of April. On the basis of only two years' observation it appears that *spurcata* will begin hatching when the total accumulated daily degrees above 60° F reach approximately 500.

LIFE HISTORY

Description of Eggs

The eggs of *D. spurcata* are laid in pods in rocky, sparsely vegetated soil (figs. 2, 3), approximately 1 to 1½ inches below the soil surface. The outer matrix of the egg pod is composed of a fluid, secreted by the female during oviposition, that hardens and coats the eggs with dirt and sand particles as shown in figure 4.

As with many species of grasshopper, the eggs are placed in the egg pod nearly horizontally with the long axis of the pod. The posterior end of the egg is fastened to the matrix. The average length of a number of field-collected egg pods ranged from 2.5 cm to 3.8 cm, with an average of 3.3 cm. The width of the egg pod varies from 5 to 8 mm and the general shape is curved. At the top of the egg pod is a porous, spongy material that forms a plug in the oviposition channel in the soil. This is about 2 to 5 mm long.

The eggs are a pale creamy yellow and reniform or banana-like in shape. For some time after the egg has been laid the chorion adheres to the egg rather firmly and is whitish in color, later becoming yellowish, then brownish prior to hatching. It is brittle and will peel off in patches. Underneath the chorion the egg is enclosed in the thin transparent vitelline membrane. The average length of the eggs is approximately 5 mm, and the average width is approximately 1.5 mm, with very little variance between eggs. The number of eggs per egg pod varies from 23 to 52 with an average of 36.

The eggs are deposited in the fall (late August to October) and remain unhatched in the ground throughout the winter months up to early or middle April. Through part of this period the egg is in diapause and shows no de-

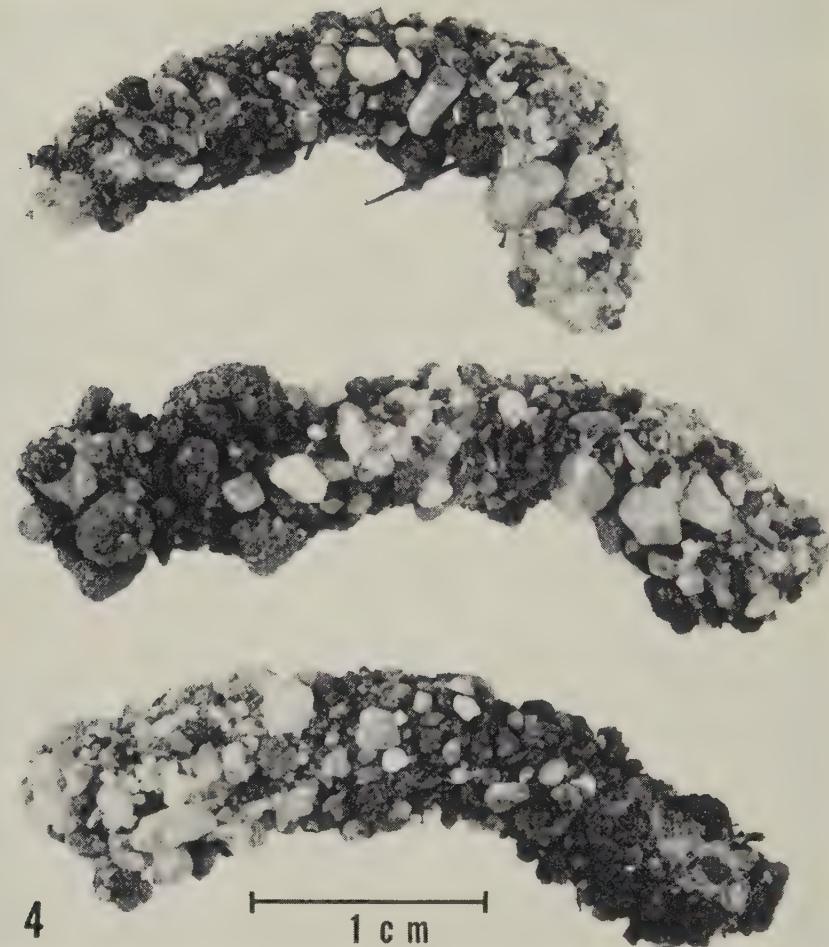


Fig. 4. Egg pods of *Dissosteira spurcata* taken from oviposition sites in the Midway Road, Alameda County study area, November, 1959.

velopment. By February or March the effect of increased temperatures and winter moisture triggers the hatching mechanism and development begins. During this period the developing embryo is visible and gradually the various external morphological characteristics can be discerned. The eyes, head and mouthparts, abdominal segmentation, and even movement can be seen with the aid of a binocular stereoscopic microscope at this time.

Hatching begins in April and continues for several weeks. In 1959, field observations showed that the spureate grasshopper hatched between April 9 and late May in northern California. Hatching usually takes place in the morning when the temperature is between 45° and 80° F.

It was once believed that grasshopper eggs were too similar to be of use in a systematic separation of the species or even the genera. Differences were noted in comparative size, shape, color, characteristic time and place of

oviposition, and the number of eggs per egg pod but these were not uniform for a species or a genus. Also size and shape of the egg pods proved to be too varied for accurate classification. Uvarov (1928) was the first to suggest that grasshopper eggs might be identified on the basis of the chorionic sculpturing. Tuck and Smith (1939) described the eggs of 48 species of grasshoppers



Fig. 5. Chorionic sculpturing of the egg of *D. spurcata*. ($\times 720$.)

and constructed a key based on the sculpturing. Sections of *D. spurcata* egg chorion were studied, using Tuck and Smith's method. The sculpturing appears as shown in figure 5.

Upon hatching and emergence from the egg the grasshopper still resembles the fully developed embryo in the egg. It is enclosed in a transparent membrane that envelopes the entire body like a sack. As the nymph is restricted in the use of its appendages by this membrane it moves to the soil surface mainly by means of wriggling, worm-like movements of the abdomen. The enveloping membrane was originally believed to be the amnion but its make-up and shape prompted Uvarov (1928) to call it a true larval skin and regard it as a regular molt and not as a continuation of the hatching process. Thus, according to Uvarov, the vermiform larva is the first larval stage. The inclusion of this process as a true larval stage would alter the total number of molts and stages, consequently most subsequent authors generally refer to it as the vermiform larva and the shedding of its skin as the intermediate molt. This molt takes place almost simultaneously with the emergence of the larvae on the soil surface.

Uvarov (1928) states that for a normal shedding of the larval skin certain conditions are necessary. A definite degree of air humidity is important to maintain the elasticity of the skin, but if too moist it becomes difficult to burst. Also common is an irregular molt when the skin ruptures in the wrong place. The hopper is unable to shed it and subsequently dies from its restricted ability to move. In several cases this skin was removed from insectary-reared specimens when the grasshopper was unable to emerge by itself.

Description of Stages

As determined from reared specimens, *D. spurcata* normally has five instars plus the vermiform stage; less than 1 per cent of the individuals go through a sixth instar before reaching maturity.

First Instar. Body length 3.8 to 7.8 mm; head 1.8 to 2.7 mm in depth and 1 to 1.6 mm wide; hind femur 2.2 to 3.8 mm long. Antennal segments 11 to 14.

The color of the newly hatched nymph is usually a mottled light tan with darker brown spots over the entire body surface. Both front legs, the inner surface of the hind femur and the labial and maxillary palpi are marked with brown bands. The hind tibia is dark brown for almost the entire length. The underside of the abdomen is a bright yellow. The tip of the antennae is reddish brown. The median carina is sharply elevated with a barely discernible concavity where the single sulcus will be in later instars. The hind femur is marked with slightly darker bands transversely across the length of the outer face. The wing pads are hardly distinguishable on the lateral edges of the meso- and metanotum.

Second Instar. Body length 7.2 to 11.2 mm; head 1.9 to 2.7 mm in depth and 1.9 to 2.1 mm wide; hind femur 4.1 to 6.2 mm long. Antennal segments 16 to 19.

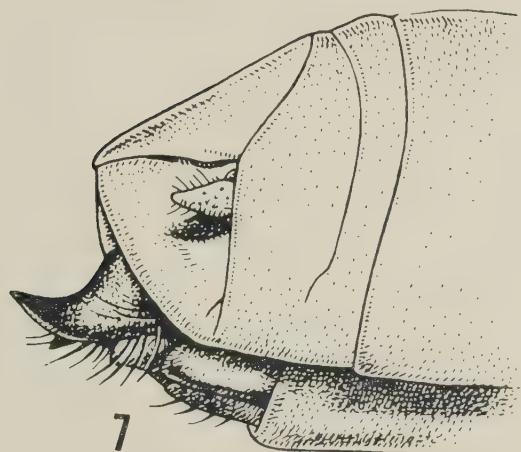
In this stage the colors begin to vary with a distinct straw yellow phase apparent. The yellow second instar nymph still has markings similar to those described for the first instar but these markings are more subdued and masked by the over-all yellow color. The majority are still the mottled tan color with a gradual darkening, appearing almost light gray. The most conspicuous external characteristic of the second stage is the dark-brown banding on the inner surface of the hind femur and the bright yellow of the abdominal venter. The median carina is approximately the same as in the first instar, the concavity is slightly more pronounced. The dark bands on the outer face of the hind femur are faded or gone. The wing pads are slightly larger with some venation slightly visible.

Third Instar. Body length 11.3 to 14.1 mm; head 4.3 to 5 mm in depth and 2.6 to 3.3 mm wide; hind femur 6.4 to 7.4 mm in length. Antennal segments 19 to 22.

The color is similar to the second instar except for a few individuals that show wide extremes from a dull orange to creamy yellow and very pale yellow to dark gray tan, almost black. The usual mottled tan color, however, still predominates. The markings on some individuals are distinct while on others, are masked and barely discernible. *D. spurcata* nymphs are distinct in appearance because of their oversized head which dwarfs the rest of the body. The wing pads are definitely larger, still directed downward, with distinct venation and appearing as lobes on the lateral rear angles of the meso- and metanotum. Median pronotal carina shows a distinct sulcus.

Fourth Instar. Body length 11.6 to 16.8 mm; head 5.2 to 7 mm in depth and 3 to 3.9 mm wide; hind femur 7.1 to 10.2 mm in length. Antennal segments 20 to 22. The body markings and colors are similar to those of the third instar but patterns are more conspicuous. The large head size is somewhat offset by the increased size of the thorax and abdomen. The median carina is sharply elevated and deeply notched. The wings are now upturned. The tegmina and wings have distinct venation that is clearly visible to the naked eye. The apex of the wings varies from a position at the front margin of abdominal segment I to past the hind margin.

Fifth Instar. Body length 16.6 to 23.2 mm; head 6.1 to 8 mm in depth and

Fig. 6. Genitalia of *D. spurcata*, male.Fig. 7. Genitalia of *D. spurcata*, female.

4 to 4.6 mm wide; hind femur 10.2 to 12.8 mm in length. Antennal segments 23 to 25.

The color and body markings are the same as in the fourth instar. The body is now in good proportion to the head. The notch in the carina is deep. The wing pads are upturned with strong venation and the apex reaches from the second abdominal segment to past the hind margin of the third.

Adult

Female (figs. 9, 10). Body length 27 to 35 mm; head 8 to 10 mm in depth and 4.5 to 5 mm wide. The tegmina exceed the end of the abdomen by 7 to 10 mm. The color is normally tan to light gray with approximately one-fifth of

TABLE 3

SEASONAL DEVELOPMENT OF NYMPHS OF *DISSOSTEIRA SPURCATA*
 SAUSSURE DURING 1959 AT THE MIDWAY ROAD STUDY AREA.
 NUMBER OF SPECIMENS COLLECTED ON EACH DATE

Date of field collection	Instar										Adult	
	I		II		III		IV		V			
	M	F	M	F	M	F	M	F	M	F	M	F
April												
9.	26	14	1	...	1
12.	27	12
16.	34	17
21.	48	20	10	4
23.	50	32	7	1
27.	44	17	11	6	1
May												
4.	18	13	7	5	...	5	1
7.	14	17	26	6	2	2	6	1
12.	4	11	11	7	9	7	3
14.	1	4	4	7	1	5	5	3	1
18.	5	1	10	12	8	7	2	3	1
21.	2	...	5	6	5	7	7	1	4
26.	1	1	5	5	4	5	8	1
June												
1.	2	..	3	4	13	5	7	5	6	...
3.	1	2	2	2	9	10	6	3	4	...
8.	1	...	4	3	2	7	6	8	...
11.	1	1	1	3	3	2	26	6
15.	1	1	...	6	8	3	14	8
18.	1	3	5	30	14
22.	2	4	24	10
29.	3	6	4	...
July												
8.	24	12	...
20.	16	14	...

the total number a pale to creamy straw yellow. The markings on the tegmina are either four or five dark-colored bands of varying width and distinctiveness. The wings are a pale yellow marked on the margins with vague darker coloration. The hind femur is marked with two or three diagonal dark bands across both the inner and outer face. The hind tibia is a pale yellow with two rows of dark-colored spines. The carina is deeply notched with the notch projected slightly forward. The yellow color on the underside of the abdomen is replaced by the color of the rest of the body. The female is a more robust insect, being larger and stockier throughout than the male. The characteristics of the female genitalia are shown in figure 7.

Male (fig. 6). Body length 23 to 29 mm; head 6.5 to 8 mm in depth and 4 to 5 mm wide; hind femur 13 to 16 mm. In general the male is small and more slender than the female, and except for the genitalia, is similar in color and body structure to the female.

Seasonal Development

Hatching of the eggs begins in early or late April and continues into late May. Nymphal development through the five instars takes 45 to 50 days. The first adults appear in early June with the males reaching maturity from one to two weeks ahead of the females. By July, males and females are equally abundant. By late June the males have begun to make their mating flight, but it is late July before mating commences. Oviposition begins in the latter part of August and continues till the middle of October. The number of adults gradually declines through October and the adult population is usually gone by the end of October, giving *D. spureata* a 6½- to 7-month life span. This period would vary somewhat in different years and different localities depending on such climatic factors as temperature and rainfall. The eggs remain in the soil throughout the winter until hatching time in April and the beginning of a new generation.

TABLE 4
DEVELOPMENTAL PERIOD AND PERCENTAGE SURVIVAL
OF *DISSOSTEIRA SPURCATA* AT DIFFERENT
CONSTANT TEMPERATURES

Item	Temperature		
	68° F	77° F	89.6° F
Number of individuals.....	50	50	50
Mean developmental time (in days).....	..	53.1	33.8
Percentage survival.....	0	42	76

Collections were made, from April 9 to July 20 in 1959, over the entire Midway Road study area at 2- to 10-day intervals. The nymphs were separated as to instar and sex and the total numbers recorded. The table constructed from these totals shows the seasonal development from hatching to maturity of *D. spureata*. The results are shown in table 3.

First instar nymphs were present from April 9 to May 21 showing a hatching period of almost 2 months, which corresponds roughly to the 2 months' oviposition period. The development of the second to fifth instar nymphs followed, with considerable overlap, a pattern of approximately seven weeks for each instar to be present, with approximately four to seven days separating the appearance of individuals of each instar. Adults first appeared June 1 and were the only stage present by the first week of July.

Development at Constant Temperatures

Since temperature is one of the most important factors affecting the development of grasshoppers, an attempt was made to rear *D. spureata* individually in cabinets under controlled temperature conditions.

Twenty eggs were placed in each of 20 pots for a total of 400 eggs. Of these, 237 hatched, or a total hatch of 59.3 per cent. Actually, more nymphs hatched, but many had difficulty breaking completely free of the egg chorion and died on the soil surface of the pots, still in the vermiform stage. Due to the relative

shortage of eggs no work was attempted on controlling the incubation temperatures and securing figures for the percentage of hatch at various constant temperatures. The highest mortality was within the first 48 hours after hatching. The eggs were placed in the pots April 8 and hatching started 17 days later on April 25, continuing over a period of 17 days until May 11.

Fifty nymphs were placed in each of three cabinets and an additional 50 in individual cages in the greenhouse. Forty newly hatched first instar nymphs were collected on April 9, in the Midway Road study area and placed in a cage in the greenhouse for comparison study. The length of time necessary for development and the proportion of survival to maturity at 68°, 77°, and 89.6° F are summarized in table 4.

It was impossible to rear any nymphs to maturity at 68° F. All but six of those at 68° F died before the first molt and five of the remaining six died before the second molt. The average period between hatch and the first molt of these six was 15 days. The last survivor went through three molts before death, 13 days to the first molt, nine to the second molt, and 11 to the third molt. Since the humidity was the same as at 77° F and all other factors identical with the other two constant temperatures, it seems likely that death was caused by the low temperature. It is significant to note that while it took longer, 44.8 days, for development under the variable 60° to 100° F greenhouse conditions than at 89.6° F, the survival rate of 84 per cent was somewhat higher than that of any of the constant temperatures. It would thus appear that between 68° and 77° F is the minimum effective temperature range for nymphal development of this species at constant temperatures, and that the spureate grasshopper shows a higher percentage of survival and faster development at temperatures well over 80° F.

It can be assumed that hot summers are conducive to more rapid development and subsequent longer oviposition periods.

Of all the nymphs reaching maturity in this study the majority went through five instars regularly in the nymphal development, showing considerable variation in their rates of development, with as much as five to six days difference in time between molts. Out of 95 that did reach adulthood only three went through a sixth instar—two from the 77° F cabinet and one from the 89.6° F cabinet. All three were females. None of those reared in the greenhouse at variable temperatures exhibited this extra instar.

Food and Feeding Habits

Grasshoppers in general do damage to range land grasses beyond the actual feeding. They cut the blades and stems near the crown, eating only a part of them. The resulting damage is far more serious than just the loss of the grass consumed. They feed closer to the ground than do livestock, subsequently retarding the growth, preventing reseeding, or even killing the plant. As a result, the soil is exposed to erosion by the effects of wind and water, particularly during drought years.

The plant life of the northern California range lands is extremely varied, with each site having its characteristic plant fauna. There were 12 species of plant life in the Midway Road study area during the developmental period of the spureate grasshopper. The three most prevalent species were: *Avena*

fatica L.—wild oats; *Hordeum murinum* L.—wall barley or farmer's foxtail, and *Brassica arvensis* L.—charlock. These comprised about 80 per cent of the total plant life in the area.

Three additional species were fairly common throughout the area, especially along the railroad tracks: *Senecio vulgaris* L.—common groundsel; *Eremocarpus setigerus* Benth.—turkey mullein; and *Grindelia camporum* Green—gum plant.



Fig. 8. Two male *D. spurcata* feeding on turkey mullein (*Eremocarpus setigerus*).

The remaining six species were scattered and sparse throughout the area: *Malva parviflora* L.—cheese-weed; *Sonchus oleraceus* L.—common sow-thistle; *Amsinckia gloriosa* Eastw.—buckthorn weed; *Convolvulus arvensis* L.—bindweed or orchard morning-glory; *Chenopodium album* L.—white pigweed or goosefoot; and *Erodium cicutarium* L' Her.—red-stem filaree.

The usual methods used for determining the food preferences and feeding habits of grasshoppers are through direct observation under natural conditions, by actual evidence of feeding on the plants themselves, and the rearing of plants and grasshoppers under artificial conditions. Direct observation is often very difficult—tedious and time consuming—but can be accomplished if one is patient and sits motionless long enough for the alerted and wary individuals to settle and begin feeding. Rearing under artificial conditions requires not only a great deal of time but also facilities, equipment, and manpower beyond the means of most investigators. Visual evidence of feeding is most often used and usually is accurate and dependable. Another more exact method was first suggested by Isely and Alexander (1949) who

reported on the possibility of analyzing grasshopper food habits by examining the crops of the insects. They pointed out that food accumulates in the crop in a state of incomplete mastication and the fragments therein are often of such size and condition that they can be recognized. Mulkern and Anderson (1959) reported on their technique by which the diet of grasshoppers can be determined by examination of the crop contents of nymphs and adults.



Fig. 9. *Dissosteira spurcata*, dark-phase adults: a, female; b, male.

The first step was to determine if different species of plants exhibited characteristics with which they could be identified in a masticated condition. In order to obtain "type" reference slides, Mulkern and Anderson (1959) first used crop contents from grasshoppers caged and fed on a single plant species. Another method of obtaining type reference slides that proved to be equal or superior to the crop contents slides was to chop the plant samples in a Waring blender to a particle size approximating that found in a grasshopper's crop. It was found that many plants have various hairs, spines, serrations, and other features which served to identify them. Using the reference slides for plant species of a particular area, grasshopper crop contents can be compared and in most cases it can be determined what plants were eaten.

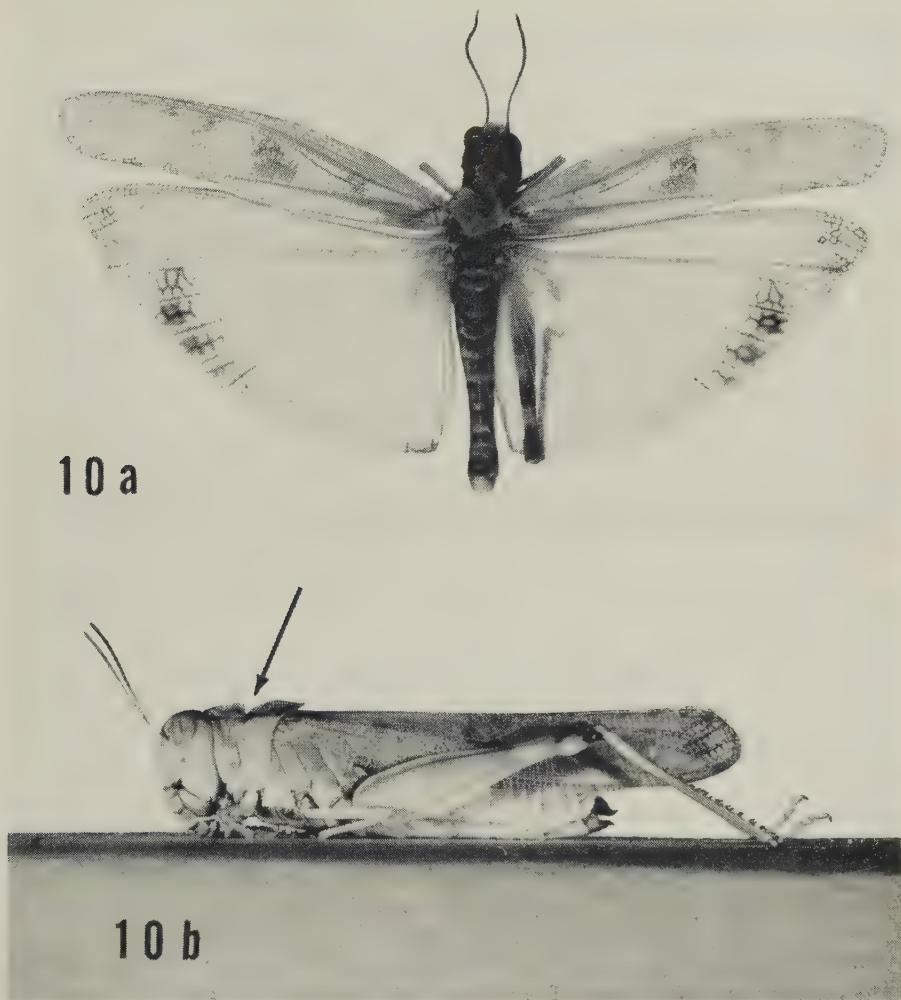


Fig. 10. *Dissosteira spurcata*, light-phase adults: a, male with wings spread; b, female.
Note distinctive pronotal sulcus.

Specific determinations cannot usually be made when various plants are eaten by the grasshopper at random, but this fact is valuable in itself.

Using the above system, type reference slides were made of the plants found in the study area and compared with crop contents of 20 *D. spurcata*. The following plants were identified: *Amsinckia gloriosa*; *Convolvulus arvensis*; *Erodium cicutarium*; *Hordeum murinum*; *Malva parviflora*; *Avena fatua*; *Sonchus oleraceus*; *Senecio vulgaris*; and *Brassica arvensis*. *Amsinckia gloriosa* and *Convolvulus arvensis* were found in three crops; all others were in only one. It is surprising that *Eremocarpus setigerus* was not found, as this was one of the favorite plant foods in later months.

Using direct observation, the following plants were recorded as being utilized for food: *Brassica arvensis*; *Eremocarpus setigerus*; *Convolvulus arvensis*; *Malva parviflora*; *Sonchus oleraceus*; *Chenopodium album*; *Avena fatua*; and *Hordeum murinum*. Figure 8 shows *D. spurcata* males feeding on *Eremocarpus*.

By the first or second week in May, especially in a year with little winter rain, most of the vegetation turns yellow and dies. Exceptions are turkey mullein and other low-growth plants. Under these conditions the grasshoppers are forced to feed on the dried wild grasses, on which they survive quite readily. As there is no available water in the area the only sources are from the juices within the plants, metabolic water or dew.

Color Phases

Early in the developmental period two distinct color types were noted. The tan-gray type with dark markings (figs. 9a, 9b) which comprised four-fifths of the population and the light to creamy-yellow individuals with light or no dark markings (figs. 10a, 10b). While the darker markings were much less pronounced on the yellow forms, they were identical in all other characteristics. These two types occurred in both sexes, and while no experimental work was done along this line it is believed that these two color types are genetically controlled and not a result of any temperature extremes or other environmental factors. These color types become noticeable from the second instar and maintain the same proportions in the population throughout development. The dark color phase was extremely effective in concealing the grasshoppers when they were in a gravel-rocky area, matching almost perfectly with the rocks on the railroad bed. Concurrently the yellow phase grasshoppers were practically invisible in the yellow grasses prevalent in the area.

It was noted that both nymphs and adults showed a tendency to depend upon their protective coloration to avoid detection when disturbed, jumping only when closely approached or burrowing into the rocky railroad bed or the grass cover. Associated species such as *Melanoplus devastator*, *Oedaleonotus enigma*, and *Trimerotropis* spp. would jump vigorously when approached.

Activity and Movement

D. spurcata shows no migration in any stage of its life cycle. Once a population has been located, it is relatively easy to mark the boundaries of the area inhabited and this area remains constant throughout the life cycle. In the Midway Road area the population remained near the hatching area for two to three weeks, gradually withdrawing from the semi-clear area to the adjacent sparsely vegetated fields. As the young reached adulthood, the area encompassed by the population had grown to include fields on either side of the original hatching area. *D. spurcata* could not generally be found 500 to 600 yards from this area. Local movement from the grass area to the bare railroad bed, road side, or road was made daily depending on the temperature. This is truly a heat-loving species, moving out onto exposed rocks and the road in an effort to absorb more heat while other species such as *Melanoplus devastator* are climbing the grass to escape the high ground temperature. Shade is



Fig. 11. Mating position of *D. spurcata*: upper, right view; lower, left view.

sometimes sought under low plants, such as turkey mullein, by *D. spurcata* when extreme temperatures are reached. At night, *D. spurcata* seeks shelter under low plants or by burrowing into the grass mat.

Flight Pattern

In flight, *D. spurcata* adults tend to move 1 to 6 feet above the ground in a zig-zag flight that usually doubles or makes a half turn back before landing. The average flight ranges from 15 to 25 yards but *D. spurcata* adults are strong fliers and capable of long sustained flight, up to 50 to 60 yards or more. On landing, they usually run a few inches and then remain motionless, generally not taking flight as quickly the second time as is sometimes common with certain other species. The male is quicker at taking flight when disturbed than the female, and will fly longer distances. The female tends to circle back and return to her original position. Adults would not readily fly when the wind exceeded about 15 miles an hour.

Mating

Mating begins in the latter part of July, although on June 18, 1959, a pair was found mating in the paper bag used to hold them while collecting. In the summer of 1958 the first mating observed was on July 30; in 1959, July 21 was the first observed mating. Prior to mating, the characteristic male hovering flight was observed in early July, 1958, and on June 22, 1959. Temperatures were much cooler in the spring of 1958 and may have delayed other life functions besides time of hatching.

This flight of the male is now believed to be the nuptial or premating flight and is characteristic of members of the genus. The hovering flight varies from several inches to several feet above ground level and usually lasts 10 to 30 seconds, occasionally longer. The male begins this flight around 10:00 a.m. after air temperatures have increased and they may be observed performing throughout the daylight hours. Middlekauff (1958) has described this flight in some detail. A single male can be seen to jump into the air a foot or two above a patch of flattened grass or a bare spot, and there he hovers in one spot with fluttering wings. The flight is noiseless for about 5 to 10 seconds then with a slower wingbeat and the abdomen pointed almost downward he begins to make a characteristic buzzing sound which lasts 10 to 20 seconds but may continue up to 35 seconds. The male then abruptly drops to the ground, moves above nervously, and makes three or four rasping noises by sharply raising the hind legs and rubbing them against the tegmina. It was noted that the caged males also made this rasping noise throughout the day. There is usually a short wait before the flight is repeated.

Only once was the nuptial flight observed to culminate in copulation. A male made his flight and while thus occupied a female moved up to the bare area below him. On landing, the male began rasping until sighting the female whereupon he began to pursue her. Both moved in quick spurts, the female remaining slightly ahead of the male. The chase continued for a foot or so until finally the female allowed the male to catch up with her. He circled her, attempting several times to mount, but each time she sidled away. He circled her again and this time was successful. The usual mating position is with

both sexes facing in the same direction with the bodies parallel. The male is on top and slightly to the right or left of the female. The left fore tarsus of the male rests upon the vertex of the female's head or on the side of the pronotum, his left middle leg clasping her tegmina at a point shortly behind her left hind coxa. The male's left hind leg rests upon the left hind leg of the female. The balance of the body of the male is to the right of the female with his two right front legs gripping the right ventral portion of the female's body. The right hind leg is braced against the ground. Figures 11a, 11b, illustrate the typical mating posture.

The mating pair is usually fairly inactive while copulating, at most a jerk of a leg or an antennal movement is all that occurs with the bulk of time being spent quiescent. The female occasionally moves around quite freely. Copulation will continue from 30 minutes up to several hours. During copulation other males, not necessarily of the same species, seem attracted and have been seen climbing onto the mating pair who, except for an occasional kick of the hind legs seems not to notice. During mating, the mating pair is relatively oblivious to all disturbances so that it is possible to approach and observe at very close quarters.

A *spurcata* female was observed resting on the bare ground when two *Cannula pellucida* males one after the other mounted her attempting to mate. The female did not move and after several fruitless attempts the *Cannula* males moved away.

Oviposition

Oviposition begins for the spurate grasshopper in the latter part of August continuing throughout the remainder of the life cycle, up through September and into October. Figure 12 shows a female ovipositing in the Midway Road study area.

There are no special climatic requirements to preclude or induce oviposition by *D. spurcata*, as is the case with *Melanoplus devastator*. There is merely the natural sequence of egg maturation followed by fertilization and the location of suitable sites. The latter is no problem since much of the surviving population remains near the previous year's oviposition area. This cycle is repeated yearly without interruption barring unforeseen decimation of the population by climate, man, or other factors.

As described earlier the preferred oviposition habitat consists of fairly loose soil, sparsely vegetated, and covered with a layer of fine to coarse gravel and rock. While usually found ovipositing singly, at the height of the egg-laying period, several to many females can be found lined up from several inches to several feet apart. The favored time for oviposition is from 9:00 a.m. to 1:00 p.m. but it can and does occur earlier and later during daylight hours.

The female spends a considerable amount of time selecting a place for depositing each batch of eggs, some attempting as many as six to eight times before being successful. One female was observed making 12 abortive beginnings before being successful; another was seen trying over and over again to oviposit in the middle of an asphalt road, moving a few inches and then trying again. The exact requirements are unknown but physical properties of the soil seem to be of greatest importance.

Females ready for oviposition become extremely restless, moving about and



Fig. 12 (top). Adult female (light-colored phase) during oviposition. Note abundance of gravel.

Fig. 13 (bottom). *D. siccata*, showing male attempting to copulate while the female is ovipositing.

making movements as if digging with the ovipositor. Even after beginning to dig, a female will sometimes stop, apparently because of unsuitable soil conditions. When the right location is found, the female rises high on the first two pairs of legs, supporting herself also by the hind pair, with the abdomen strongly arched and its end perpendicular to the surface of the soil. The process of digging by a female grasshopper is described by Uvarov (1928). The main work is done by the valves of the ovipositor, which make two kinds of movements. At first, they are all collected together, forming a wedge-like tool that enters the soil under the pressure of the abdomen, then the upper and lower valves open and the hole is widened. The valves are then closed and forced deeper into the soil. This process is repeated over and over. In this way a burrow is made with the abdomen elongating and the ovipositor entering deeper and deeper into the soil. The degree of abdominal extension is amazing, the length doubling and tripling throughout the entire process. To give the burrow a circular shape, the female contracts the abdomen from time to time and corrects the work already done by twisting the end of the abdomen through 90 degrees, first right then left.

When the burrow is ready, oviposition begins. First the abdomen is slightly contracted and the female begins to emit the foamy material secreted by the accessory glands. The eggs, enveloped in a thin, foamy film, appear one after another through the aperture in the closed valves; they are laid with their micropylar ends downward. The abdomen gradually contracts, and at the completion of the process the female withdraws her distended abdomen and preens it with her hind tibia as it compresses back to its normal length. When all the eggs are laid, the foamy material is emitted and this serves to form the stopper, or lid, of the egg pod. The function of the secretion of the accessory glands is protective, especially from excessive moisture or drought. The egg pod is further strengthened by the secretion sinking into the adjacent layer of soil, hardening and forming a very strong and hard covering. By March, or just prior to hatching, this egg pod matrix has been dissolved by the action of winter moisture.

The entire process of oviposition lasts about an hour. After completion the female preens her abdomen, then carefully smooths the small area of soil directly over the egg pod with her hind legs, removing all signs of her activity. This takes several seconds and when completed she flies away.

During the process of egg deposition it was almost impossible to interrupt the female, even when physically pulling on the tegmina or pushing her. Females are easily frightened while driving the ovipositor in, but once they have settled down to laying the eggs their instinctive fear is overridden by the stronger instinct of egg laying. Even when a female is finished and going through the ritual of smoothing the area with her hind legs, she can be pushed about, merely struggling to resume her task.

In numerous cases the male was in the mating position on the ovipositing female with his abdomen curled under and up into the canopy made by the female's wings and tegmina (fig. 13). The males in this position likewise were not frightened easily. The male was not observed mating with the female upon completion of oviposition but this has been reported as normal with other species in the genus.

Toward the end of the oviposition period, there are many more females than males. Males die off first, being several weeks older than the females. The death of the females concludes the life cycle, with the latest female observed on October 27, 1958.

PARASITES AND PREDATORS

Observations of predators and parasites of *D. spurcata* yielded little in the way of new or even specific identification. No egg destruction was noted except for claw marks in the egg pod area, indicating possible rodent or mammal destruction of egg pods. A species of mite of the genus *Euthrombidium* was common on the wings, leg joints, and neck region of *D. spurcata* but no deaths or even reduction in vigor was noted of those so affected. Through dissection of a number of adults, dipterous larvae were found infesting the body cavity of several adults. These could be identified only as belonging to the Sarcophagidae and Tachinidae. One of the Tachinidae maggots was tentatively identified as being in the genus *Hemithrixion*. Specimens of a few adult sarcophagid flies were reared from caged *D. spurcata* adults. These flies were placed in the Aeridiophaga group, but further study will be necessary before specific identification can be obtained for either the larvae or the adults.

Digger wasps (*Tachysphex* spp.), as described by Newton (1956), were active in the study area but were not observed attacking *D. spurcata*. Robber flies (*Erax* spp.), fence lizards (*Sceloporus* spp.), and numerous birds were noted attacking both nymphal and adult grasshoppers. Another factor, in the Midway Road study area, is the number of *D. spurcata* killed on the road by vehicles.

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LITERATURE CITED

- BARNES, O. L.
1955. Effect of food plants on the lesser migratory grasshopper. *Jour. Econ. Ent.* **48**(2):119-24.
- BURMEISTER, K. H. K.
1838. *Handbuch der Entomologie*. C. F. Enslin, Berlin **2**(2):756 pp.
- BRUNER, L.
1893. The more destructive locusts of America north of Mexico. U. S. Dept. Agr., Div. Ent., Bul. **28**, 40 pp.
1897. Grasshopper report for 1895. U. S. Dept. Agr., Div. Ent., Bul. **7** (new series): 31-35.
1905. The Acrididae. *Biologia Centrali-Americanica. Insecta-Orthoptera* **2**:1-342.
- CALIFORNIA COÖPERATIVE INSECT REPORT
1958. Cooperative economic insect report. U. S. Dept. Agr., Plant Pest Contr. Div. **8**(36):776-92.
- COQUILLETT, D. W.
1885. Report of the locusts of the San Joaquin Valley, California. U. S. Dept. Agr., Rpt. Comm. Agr. pp. 289-303.
1892. Report of the locust invasion of California in 1891. U. S. Dept. Agr., Div. Ent., Bul. **27**:34-57.
- ESSIG, E. O.
1956. Insects of western North America. Macmillan Co., New York, 1035 pp.
- GURNEY, ASHLEY B., and H. F. STROHECKER
1959. Some Californian oedipodine grasshoppers, particularly three species given the specific name *occidentalis* by Lawrence Bruner. *Brook. Ent. Soc.* **54**(3):77-82.
- HARPER, R. W.
1950. Grasshopper control. California Dept. Agr. Bul. **39**(4):197-99.
- 1952a. Grasshoppers in California. California Dept. Agr. Bul. **41**(2):105-14.
- 1952b. Grasshoppers of economic importance in California. California Dept. Agr. Bul. **41**(3):153-75.
- HENDERSON, W. W.
1924. A taxonomic and ecological study of the species of the subfamily Oedipodinae (Orthoptera-Acrididae) found in Utah. *Utah Agr. Exp. Sta. Bul.* **191**, 150 pp.
1931. Crickets and grasshoppers in Utah. *Utah Agr. Exp. Sta. Cir.* **96**, 38 pp.
- ISELY, F. B., and G. ALEXANDER
1949. Analysis of insect food habits by crop examination. *Science* **109**(2822):115-16.
- LARIVERS, I.
1948. A synopsis of Nevada Orthoptera. *Amer. Mid. Nat.* **39**(3):652-720.
- LATREILLE, P. A.
1825. Familles naturelles du règne animal, exposées succinctement et dans un ordre analytique, avec l'indication de leurs genres. J.-B. Baillière, Libraire, Rue de L'École De Médecine, No. 14. Baudouin Frères, Rue de Vaugirard, No. 36. Paris, 570 pp.
- MERRIAM, C. H.
1898. Life zones and crop zones of the United States. U. S. Dept. Agr. Bul. **10**, 79 pp.
- MIDDLEKAUFF, W. W.
1958. Biology and ecology of several species of California rangeland grasshoppers (Orthoptera: Acrididae). *Pan-Pacif. Ent.* **34**(1):1-11.
1959. Some biological observations on *Sarcophaga falciformis* Aldrich, a parasite of grasshoppers (Diptera: Sarcophagidae). *Annals Ent. Soc. Amer.* **52**: (in press).
- MULKERN, G. B., and J. F. ANDERSON
1959. A technique for studying the food habits and preferences of grasshoppers. *Jour. Econ. Ent.* **52**(2):342.
- NEWTON, R. C.
1956. Digger wasps, *Tachysphex* spp., as predators of a range grasshopper in Idaho. *Jour. Econ. Ent.* **49**(5):615-19.

- NEWTON, R. C., and A. B. GURNEY
1957. Distribution maps of range grasshoppers. *Dissosteira carolina*, *D. longipennis* and *D. spurcata*. Cooperative Economic Insect Report, U. S. Dept. Agr. 6(38): 939-40.
- REHN, J. A. G.
1945. The status of Stals *Oedipoda venusta*, 1861. Ent. News 56:132.
- REHN, J. A. G., and M. HEBARD
1906. A contribution to the knowledge of the Orthoptera of Montana, Yellowstone Park, Utah and Colorado. Proc. Acad. Nat. Sci. Phila. 58(1):358-418.
1909. An orthopterological reconnaissance (*sic*) of the southwestern United States. Part 3: California and Nevada. Proc. Acad. Nat. Sci. Phila. 61(1):409-83.
- ROCKWOOD, L. P.
1925. On night flying and attraction to light in Aceridiidae and the relation of meteorological conditions thereto. Pan-Pacif. Ent. 2(1):36-38.
- SAUSSURE, H.
1884. Prodromus Oedipodiorum Insectorum Ex Ordine Orthopterorum. Soc. De Phys. Et. Hist. Nat., Genève, Mèm. 28(9), 254 pp.
- SCUDDER, S. H.
1876. Report on the Orthoptera collected by the United States geographical surveys west of the one hundredth meridian, under the direction of Lieutenant G. M. Wheeler, during the season of 1875. Ann. Rpt., U. S. Chief Engin. 1875-1876 (App. JJ):278-95.
1900. Catalogue of the described Orthoptera of the United States and Canada. Proc. Davenport Acad. Nat. Sci. 8, 101 pp.
1901. Alphabetical index to North American Orthoptera. Boston Soc. Nat. Hist. 6, 436 pp.
- SHOTWELL, R. L.
1941. Life histories and habits of some grasshoppers of economic importance on the Great Plains. U. S. Dept. Agr. Tech. Bul. 774, 48 pp.
- THOMAS, C.
1880a. Notes on Orthoptera. Canad. Ent. 12 (11):221-24.
1880b. Locust ravages in California. Second Rpt. U. S. Ent. Comm. pp. 242-59.
- TUCK, J. B., and R. C. SMITH
1939. Identification of the eggs of mid-western grasshoppers by the chorionic sculpturing. Kansas State Agr. Exp. Sta. Tech. Bul. 48, 39 pp.
- URBAHNS, T. D.
1920. Grasshopper control in the Pacific states. U. S. Dept. Agr. Farmers' Bul. 1140, 16 pp.
- UVAROV, B. P.
1928. Locusts and grasshoppers: A handbook for their study and control. Imp. Bur. Ent. London, 352 pp.
- WAKELAND, C.
1958. The high plains grasshopper: A compilation of facts about its occurrence and control. U. S. Dept. Agr. Tech. Bul. 1167, 168 pp.

